BREEDING BIOLOGY OF THE ZONE-TAILED HAWK AT THE LIMIT OF ITS DISTRIBUTION

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ABSTRACT.—Twelve zone-tailed hawk (Buteo albonotatus) nest stands in eight territories were studied in northcentral New Mexico during 1990-92 to determine the nesting chronology, nesting habitat, diet, and productivity of a population that is at the limit of the species' distribution. Zone-tailed hawks arrived on the study area from late March to early April and their breeding season ended in mid- to late September when the family unit left the nest stand. All nest stands were in ponderosa pine (Pinus ponderosa) forests located in the bottom or on the slopes of steep-walled canyons, and frequently in close proximity to cliffs. Stand basal area averaged 23.8 m²/ha and percent canopy closure averaged 69.2% (N = 10). Nest trees (N = 8) were large, averaging 23.8 m in height and 59.8 cm diameter at breast height (dbh). The diet consisted of a mixture of mammalian, avian and reptilian prey species that are common in the study area. During 1990 and 1991 only one of six known territories successfully fledged two and one young, respectively. During 1992 two new territories were located and these were the only successful nests (fledged one and two young). Although sample sizes are small, the productivity that we recorded is the lowest reported productivity of any zone-tailed hawk population. Reasons for the low productivity are unknown.

KEY WORDS: breeding chronology; Buteo albonotatus; diet; habitat; New Mexico; productivity; zone-tailed hawk.

Biología reproductiva de Buteo albonotatus en el límite de su distribución

RESUMEN.—Se estudiaron doce nidos de Buteo albonotatus en ocho territorios ubicados en el centro norte de New Mexico, entre 1990 y 1992. Se determinó la cronología y hábitat de nidificación, dieta y productividad de una población que se encuentra en el límite de distribución de la especie. Buteo albonotatus llegaron al área de estudio a fines de marzo y a principios de abril y su estación reproductiva finalizó la última quincena de septiembre, cuando la familia dejó el nido. Todos los nidos se localizaron en bosques de Pinus ponderosa ubicados en el fondo o sobre laderas de cañones amurallados y frecuentemente cercanos a riscos. El promedio de áreas basales de las agrupaciones vegetales es de 23.8 m²/ha y el porcentaje promedio de la cobertura del dosel es de 69.2% (N=10). Los nidos se encontraban ubicados en árboles a una altura promedio de 23.8 m y 59.8 cm dbh (N = 8). La dieta consistió de una mezcla de presas de mamíferos, aves y reptiles que son comunes en el área de estudio. Durante 1990 y 1991, solamente uno de los seis territorios conocidos produjo dos y un volantones, respectivamente. Durante 1992 dos nuevos territorios fueron localizados con una producción de un y dos volantones. Aunque el tamaño de la muestra es pequeño, la productividad registrada es la más baja reportada para una población de B. albonotatus. Razones para esta baja productividad son desconocidas.

[Traducción de Ivan Lazo]

The zone-tailed hawk (Buteo albonotatus) is a relatively uncommon and widely distributed raptor of the southwestern United States and Latin America (Brown and Amadon 1968, Palmer 1988). Only about five percent of its range is in the U.S., and it has been estimated that only 80-100 nest stands of this species are known in this region (Millsap 1981, Snyder and Glinski 1988). In the U.S., the zonetailed hawk is most commonly found in southern and central Arizona and New Mexico, although nesting pairs have been documented in Texas and southern California (Oberholser and Kincaid 1974, Matteson and Riley 1981, Snyder and Glinski 1988). It is most commonly found in mountainous areas and lowland riparian zones, and is often associated with steep terrain. Nest-stand vegetation is varied, but deciduous riparian and montane coniferous forests are the most common types reported. The zonetailed hawk is a year-round resident in lower latitudes but is thought to be migratory throughout the northern third of its range, though winter sightings in this area are not uncommon (Palmer 1988). Limited information is available on the species' breeding biology (Matteson and Riley 1981, west Texas; Millsap 1981, westcentral Arizona; Hiraldo et al. 1989, Durango, Mexico), and no published information is available on the ecology of zone-tailed hawk populations at northern range boundaries.

In this paper, we describe characteristics of the breeding biology of zone-tailed hawks nesting in coniferous forests in northcentral New Mexico that we observed during the 1990–92 breeding seasons. This population is at the extreme northern border of the species' range. We estimated the density of nesting pairs in one portion of the study area and annual reproductive success. We also described the breeding chronology, nest-stand characteristics, and nesting season diet of the zone-tailed hawk in this area.

STUDY AREA

The study was conducted in the Jemez Mountains and adjacent Pajarito Plateau of northcentral New Mexico. This area is characterized by rough terrain dissected by steep-walled canyons at regular intervals. The vegetation at higher elevations is dominated by ponderosa pine (Pinus ponderosa) and mixed conifer forests, with pinyon-juniper woodland dominating the lower elevations. Drainages contain riparian habitats dominated by Douglas fir (Pseudotsuga menziesii) and ponderosa pine, with cottonwoods (*Populus* spp.) present at lower elevations. The vegetative characteristics of this area are described in detail in Kennedy (1991). This area encompasses approximately 650 000 ha and is managed primarily by the U.S. Forest Service, Santa Fe National Forest, the U.S. Park Service, Bandelier National Monument (BNM), and Los Alamos National Laboratory.

METHODS

Nest Searches, Breeding Chronology and Productivity. Prior to the 1990 nesting season, we collected all available information on historical occurrences of the zone-tailed hawks in the study area. This database included

information collected from the New Mexico Ornithological Society (NMOS) nest cards, a local ornithological society (Pajarito Ornithological Society), and entries in the wildlife sightings database from BNM (C. Allen pers comm.), as well as records from professional biologists (D Crowe unpubl. data, T. Johnson unpubl. data, P.L. Kennedy unpubl. data). We used this database to design nest surveys and as preliminary information on the nesting chronology of the zone-tailed hawk in the study area.

During July to August 1990, July to September 1991 and from 22–29 July in 1992, all historically active nest stands and areas of frequent sightings were searched for signs of zone-tailed hawk nesting activity and to estimate reproductive success (number of bandable young). Road and foot surveys and taped broadcasts of conspecific calls were used in these areas to aid in the detection of nesting hawks. In July 1991, an exhaustive search of BNM (13254 ha) was conducted for active nests to estimate the density of breeding territories in an area with minimal human-induced landscape alterations. All forested habitats were searched with equal effort.

Nest Stand Habitat. The dominant vegetation type, as characterized by the canopy species, and general topographic features were recorded at all nest stands (N = 12). A nest stand is defined as the area surrounding a nest tree, including vegetative and topographic features used by a nesting pair during the entire nesting season exclusive of foraging areas. Elevation and topographic location were determined from nest locations plotted on 7.5 min U.S. Geological Survey maps. The basal area (BA; m²/ha) and percent canopy closure (% CC) were measured at five points in nine of the 12 nest stands. These points were the nest tree, and points 50 m from the nest tree in each of the cardinal directions. The stand % CC and BA are presented as the average of the five measurements. The BA of each canopy species was measured with a Relaskop using a basal area factor of two (Wenger 1984) and % CC was measured with a convex spherical densiometer (Lemmon 1956, 1957). The aspect of the nest stand was measured at 10 of the 12 nest trees. Nest tree height (m), and diameter at breast height (dbh [cm]) were measured at eight nest trees, and nest height, aspect of the nest structure, and the location of the nest within the nest tree was recorded when the nest structures were still present (N = 7). All height measurements were made with a clinometer.

Diet. Prey remains and castings were collected at least twice at each occupied nest stand (any site where at least one adult exhibited nesting behavior, i.e., defensive vocalizations, addition of greenery to nest structures) during 1990 and 1991. Prey remains collected at four nests from 1986–90 in the course of other raptor studies were included in the analysis of prey items. Remains were identified to genus and species when possible, and a sample of the castings collected were analyzed for the presence of reptilian, avian, and mammalian prey.

In addition, prey deliveries were monitored for 2-3 d/wk for 5 wk (July to early August; last week of the nestling period and the first 4 wk of the fledgling-dependency period) at Nest 1 which was the only nest in the study area that successfully produced nestlings during both 1990 and 1991. During both years, Nest 1 was monitored

by one observer (DC) for 4-12 hr each day with a Celestron C90 telescope. The observer was in a blind located approximately 200 m up slope from the nest tree. Prey delivery rates were calculated for each sample period and converted to daily rates assuming 13.5 hr/d which is the average daylength in this area during July and early August (Kennedy 1991).

RESULTS AND DISCUSSION

Nest Searches. A total of 10 nests were located in six territories (Nests 1–6) on this study site during 1990 and 1991. We assumed that three of the territories (Nests 2, 4, and 6) contained alternate nest stands. This assumption was based on the close proximity of the alternate nests (<2 km) and the absence of simultaneous occupancy during a breeding season. In 1992 two additional nest stands (Nests 7 and 8) on two territories were located.

Nesting Density. Two occupied nest stands (Nests 3 and 4) were located in BNM during the 1991 exhaustive survey. Nesting density, based on the two occupied nests, is estimated to be roughly one pair/6 627 ha or 1.51 pairs/100 km². This density estimate is based on the untested assumption that all occupied sites were located during the survey. Also, because of the small sample size of nests we cannot assume that this density estimate is representative of the nesting density throughout the study area.

Snyder and Glinski (1988) report that zone-tailed hawk nests are rarely closer together than 16 km. How they arrived at that conclusion is not evident in their review paper. However, our results do not support that generalization. The minimum distance between two active nests in our study was 3.6 km and the average nearest neighbor distance was 5.4 km (± 2.0 km; N=8). The differences between our results and their conclusions may be attributed to differences in densities of linear riparian habitat as compared with contiguous montane ponderosa pine forests.

Breeding Chronology. Zone-tailed hawks have been observed on our study site as early as the last week in March, and have been recorded regularly during early April (T. Johnson pers. comm., BNM wildlife sightings database). These data suggest that the zone-tailed hawk probably arrives in the breeding area in northcentral New Mexico between late March and mid-April. The first sightings of birds in this study area are consistent with reported arrival dates in other areas (Millsap 1981, Palmer 1988).

Two courtship displays for this species have been

reported: high-circling with occasional flapping and calling (Palmer 1988), and sky-dancing (Oberholser and Kincaid 1974). We observed these displays in late April 1985, late May 1986, and in early August 1990. Courtship likely begins when both adults arrive in their territory and apparently continues throughout the breeding season. The courtship period is still poorly understood, and dates of courtship activity in this species are poorly documented.

Using an estimated incubation period of 35 d (Newton 1979) and back dating from the date we observed fledging, the approximate date of egg laying at Nest 1 was 1 May in 1990, and between 1-7 May in 1991. These dates are also consistent with reports of egg-laying in other areas, which range from 29 March to 17 May (Millsap 1981, Palmer 1988). The hatch dates in our study area, as determined from estimates of nestling ages and observed fledging dates at Nest 1, are estimated to be in the first week of June in 1990, and between 4 and 11 June in 1991. Millsap (1981) found that over 50% of eggs in southeastern Arizona hatched by 10 June and all nests had hatched by 27 June.

The young that we observed at Nest 1 remained in the nest for 38–42 d. This observation is consistent with Newton's (1979) report of a 35–42 d nestling period. The young left Nest 1 on 12 and 15 July of 1990 and 1991, respectively. The first prolonged flight by the young was on 20 July 1990 and 30 July 1991 when they were approximately 6–8 wk old. The young at the two successful nests in 1992 (Nests 7 and 8) had recently fledged when we conducted our nest surveys in late July. Millsap (1981) reported that 50% of zone-tailed hawks in westcentral Arizona had fledged by 28 July, and all had fledged by 10 August. For one nest in Durango, Mexico, Hiraldo et al. (1989) reported a fledging date of July 17.

The end of the fledgling-dependency period was not observed in 1990 or 1992, but in 1991, the fledglings were last observed in the Nest 1 stand with an adult on 12 September. This corresponds with a fledgling-dependency period of approximately 8 wk. Hiraldo et al. (1989) reported a fledgling-dependency period of 4 wk for a nest in Durango, Mexico. The length of this period is probably quite variable and is difficult to estimate from observations of only two nests and no radio-telemetry data on juveniles.

Between 12 and 28 September 1991 all family members left the Nest 1 stand. This is again in

agreement with information on departure dates observed in westcentral Arizona, where all territories were unoccupied by 3 October (Millsap 1981). There have been no observations of zone-tailed hawks in the study area after late September.

Nest Stand Habitat. Similar to Millsap's (1981) observations in westcentral Arizona, all of the 12 nest stands we located were in the bottom or on the slopes of steep-walled canyons and frequently in close proximity to cliffs. The dominant vegetation in all nest stands was ponderosa pine/oak (Quercus spp.) or ponderosa pine/douglas fir/oak. Although riparian habitat occurs in the study area, no nest stands were located in this habitat type. This is in contrast with Millsap's (1981) study area where 92.8% (N = 26) of the nest stands were in deciduous riparian forests and 7.2% (N = 2) were in ponderosa pine forests. These study area differences in nest stand habitat are probably a result of differences in nesting habitat availability. For example, montane conifer forest communities were 0.3% of Millsap's (1981) study area and 43.7% of our study area (M.S. Siders and P.L. Kennedy unpubl. data). Deciduous riparian forests were the most abundant forested habitat in Millsap's (1981) study area (0.8% of study area). We do not have estimates of deciduous riparian forest availability in our study area but it is considerably less abundant than the montane conifer communities.

All nest stands were between 1936 and 2316 m in elevation. In westcentral Arizona most zone-tailed hawk nest stands were above 1100 m elevation (Millsap 1981). Stand basal area averaged 23.8 m 2 /ha (SD = 3.4) and % CC averaged 69.2% (SD = 6.5). No comparable habitat data are available from other study areas.

All of the nest trees were ponderosa pine and the average height and dbh of the nest trees were 23.8 m (SD = 6.0) and 59.8 cm (SD = 9.1), respectively. The two ponderosa pine nest trees measured by Millsap (1981) were comparable in size to those we measured averaging 22.9 m (SD = 1.2) in height and 63.5 cm (SD = 0.4) in diameter. Eight of 11 nest stands in the Big Bend area of west Texas were also in ponderosa pine but no nest stand measurements are available for these sites (S. Matteson et al. unpubl. data in Snyder and Glinski 1988).

The nest structures were all located in the upper portion of the canopy ($\bar{x} = 90.6\%$ [SD = 0.04] of the tree height) at an average height of 22.9 m (SD =

5.1). Millsap (1981) reported nest heights of 19.8 m (SD = 0.3, N = 2). The aspects of the nests in this study were west (N = 5), north (N = 1), or east (N = 1), and the structures were constructed of sticks and lined with greenery. No comparable nest aspect data are available from other study areas.

Diet. Remains from 26 prey items were collected and identified (Nests 1 and 3-5) and 26 of 105 castings were analyzed (Nests 1 and 3-5). In addition, a total of 84 prey deliveries were observed at Nest 1 (52 in 1990; 32 in 1991) during a total of 175.5 hr of observation (87.5 in 1990; 88 in 1991). Table 1 summarizes the diet data collected at Nest 1 where all three methods of diet analysis were used. Table 2 is a list of the prey taxa used by zone-tailed hawks during the nesting season in our study area. It is a composite list based on all three dietary methods and all diet samples.

At Nest 1, reptiles accounted for 26.2, 0, and 87.5% of deliveries, prey remains, and castings, respectively. Mammalian taxa accounted for 41.7, 27.3, and 87.5% of deliveries, prey remains, and castings, and avian taxa accounted for 23.8, 72.7, and 81.3% of deliveries, remains, and castings, respectively (Table 1). The discrepancy between the occurrence of reptiles in deliveries, remains and castings at Nest 1 may result from the tendency of zone-tailed hawks to entirely consume reptilian prey, leaving few remains. This may result in reptiles being underrepresented in raptor diets (Marti 1987, Rosenberg and Cooper 1990). Avian prey are probably overrepresented in remains because of the visibility of their remains (Marti 1987, Rosenberg and Cooper 1990).

Thirteen genera/species were identified in the diet (Table 2). Our data and food habits data collected in other studies (Snyder and Wiley 1976, Sherrod 1978, Millsap 1981, Hiraldo et al. 1991) indicate that the zone-tailed hawk has a broad diet, including many vertebrates and some invertebrates. All populations take a mix of mammals, birds, and herpetofauna, but as expected, the percentage of these taxa in the diet varies between populations. The variation is probably a function of sampling method, nest sample size and local prey availability in a variety of habitat types.

The average prey delivery rates at Nest 1 in 1990 and 1991 were 8.0 prey/d (SD = 2.8; N = 12 d) and 4.8 prey/d (SD = 2.5; N = 9 d), respectively. The differences in the rates between years are prob-

Table 1. Dietary data collected at the only successful zone-tailed hawk nest (Nest 1) in the Jemez Mountains, New Mexico during 1990 and 1991.

Метнор	N^a	PREY TAXA	% of Dietb
Prey deliveries	22	Reptiles	26.2
	14	Crotaphytus sp.	16.7
	1	Sceloporus sp.	1.2
	7	Unidentified Lizard	8.3
	20	Birds	23.8
	2	Colaptes auratus	2.4
	1	Aphelocoma coerulescens	1.2
	1	Turdus migratorius	1.2
	2	Tanager-size bird	2.4
	5	Loxia curvirostra	5.9
	8	Finch-size bird	9.5
	1	Unidentified birds	1.2
	35	Mammals	41.7
	33	Tamias sp.	39.3
	2	Sciurus variegatus	2.4
	7	Unidentified Prey	8.3
Total	84	ŕ	100.0
Prey remains	0	Reptiles	0.0
	8	Birds	72.7
	1	Chordeiles minor	9.1
	2	Colaptes auratus	18.2
	1	Cyanocitta stelleri	9.1
	1	Unidentified jay	9.1
	1	Loxia curvirostra	9.1
	2	Finch-size bird	18.2
	3	Mammals	27.3
	1	Sylvilagus sp.	9.1
	2	Tamias sp.	18.2
Total	11	1	100.0
Castings	14	Reptiles	87.5
	13	Birds	81.3
	14	Mammals	87.5
Total	16		100.0

^a N is the number of deliveries, prey remains, or castings in which each taxa is represented. All samples were collected during 1990 and 1991.

ably due to differences in number of young being fed (two in 1990 and one in 1991). Hiraldo et al. (1989) reported a mean prey delivery rate of 5.9 prey/d (SD = 2.8; N = 10 d) during the post-fledging period at a zone-tailed hawk nest in Durango, Mexico where two young fledged.

Most of the prey were delivered midday between 09:00 and 17:00 H during both years (90.4% of total deliveries in 1990 and 78.1% in 1991). This diurnal pattern probably reflects the activity patterns of some

of its principal prey, lizards and medium-sized diurnal mammals (Table 1) which are more active during the warmer portions of the day in this study area (P.L. Kennedy and J.L. Morrison unpubl. data).

At Nest 1, the smaller parent (presumably the male) made almost all of the prey deliveries (93.8% in 1990 and 96.8% in 1991) and the majority of these deliveries (83.3% and 93.5% in 1990 and 1991, respectively) were brought directly to the nest without a transfer to the larger parent (presumably the

^b For the prey deliveries and prey remains this represents the percent of individuals observed. For the castings this represents the percent of the castings in which each taxon is represented.

Table 2. Prey taxa^a of zone-tailed hawks nesting in the Jemez Mountains, New Mexico during 1990 and 1991.

TAXA	No. Nests ^b	
Reptiles	-	
Crotaphytus sp.	2	
Sceloporus sp.	1	
Birds		
Chordeiles minor	1	
Colaptes auratus	1	
Cyanocitta stelleri	1	
Aphelocoma coerulescens	1	
Turdus migratorius	1	
Loxia curvirostra	2	
Mammals		
Sylvilagus sp.	1	
Tamias sp.	2	
Sciurus variegatus	1	
Sciurus aberti	1	
Peromyscus sp.	1	

^a Prey taxa were identified from observations of prey deliveries at Nest 1 during 1990-91 or analyses of prey remains collected at all occupied nests from 1986-91.

female) upon entering the nest stand. The female was in the nest stand throughout most of the observation period but her primary role in food provisioning was to feed the prey to the nestlings after the male delivered it to the nest. She apparently was not involved in food provisioning after the young were self-feeding. As Hiraldo et al. (1989) suggest, the zone-tailed hawk, like other raptors, appears to have sex role partitioning during brood rearing.

Reproductive Success. The 1990–92 reproductive success of the zone-tailed hawk in the Jemez Mountains was low. Four of six territories were occupied in 1990–91 and five of eight territories in 1992. In 1990 and 1991 one territory (Nest 1) produced two and one young, respectively, and in 1992 two territories (Nests 7 and 8) produced three young in total. The average reproductive success for the three years was 0.45 yg/occupied territory (SD = 0.18).

The low reproductive success observed in 1990–92 is probably an accurate representation of the population productivity during this period and not anomalous. The first successful nesting attempt re-

corded in this area occurred in 1985 and that nesting territory has not successfully produced young since that year. Another nest successfully fledged young in 1989, but has been unsuccessful since. The one nest that was successful in both 1990 and 1991 was successful for six consecutive years (1986–91) but failed prior to hatching in 1992, and failed in the nestling period in 1993 (T. Dean unpubl. data).

In west Texas, Matteson and Riley (1981) reported productivity of 1.14 young/occupied territory in 1975 and 0.77 young/occupied territory in 1976. The average reproductive success for 1979 and 1980 in westcentral Arizona (Millsap 1981) was 1.9 yg/occupied territory (SD = 0.71). Although sample sizes are small, the productivity that we recorded is the lowest reported productivity of any zone-tailed hawk population. In the absence of survival and immigration rate data, we cannot evaluate if this rate of reproduction is sufficient to sustain this population.

The reason for the low productivity in this population during 1990-92 is unclear. It might be an artifact of the small sample size or some unidentified local factor that influenced the 1990-92 nest success, such as low food availability and/or high nest predation. However, populations at range margins generally exhibit lower productivity and survivorship than populations nearer the center of a species' range, and such outlying populations may serve as a sink for surplus individuals from central populations (Newton 1979, Snyder and Glinski 1988, Howe et al. 1991). These outlying populations may not be capable of producing enough offspring to replace adults, and such populations may only remain intact as long as there is a surplus of individuals from centrally located populations that regularly disperse to such 'sink' populations (Pulliam 1988, Howe et al. 1991). Populations such as the one we observed may be located in areas of marginal habitat that only allows for successful reproduction in exceptional years.

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^b Number of occupied territories where this taxon was observed in either a prey remain or prey delivery during 1986-91.

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